



The effects of pH on phosphorus utilisation by chickpea (*Cicer arietinum*)

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Abstract Chickpea (*Cicer arietinum*) is known to secrete organic anions. We investigated its effectiveness in obtaining P over a range of pH values.

Methods We grew two cultivars of chickpea, supplied with either ammonium or nitrate nitrogen, at 10 levels of applied P, and at four initial pH values. We measured plant weight, P concentration in the tops, and rhizosphere pH. We compared the results with those previously obtained for lucerne (*Medicago sativa*), mustard (*Brassica campestris*) and rice (*Oryza sativa*).

Results Above an initial $\text{pH}_{\text{CaCl}_2}$, of about 5, rhizosphere pH decreased; below this value it increased. The changes in pH were proportional to the amounts of P applied. They were greatest at high levels of applied P. Best growth occurred when the initial $\text{pH}_{\text{CaCl}_2}$ was 5.9 and when the rhizosphere $\text{pH}_{\text{CaCl}_2}$

was close to 5. Plots of growth against plant shoot P concentration showed little effect of low pH suggesting that aluminium toxicity was only of minor importance. Nevertheless, plant weight was severely depressed by low pH.

Conclusions The mechanism of P uptake for chickpea seems to differ from that for lucerne, mustard and rice. The way that the charge on the phosphate ions is balanced seems to depend on the soil pH. Further, uptake is much more markedly depressed by at low pH.

Keywords Chickpea · Soil reaction · Rhizosphere pH · Phosphorus uptake · Aluminium toxicity · Phosphorus uptake mechanism

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Introduction

The classical view is that availability of phosphate is greatest near pH 7 and decreases with decreasing pH. This view was questioned by one of us (Barrow 2017). It was argued that the effects of pH on the rate of uptake by roots was more important than effects on soil chemistry; that the outcome was opposite to the classical view; and that lowest availability is at high pH. This argument was rejected by Penn and Camberato (2019) who strenuously defended the classical view. However, we then showed (Barrow et al. 2020) that for lucerne (*Medicago sativa*), mustard (*Brassica campestris*) and rice (*Oryza sativa*), the

optimum initial $\text{pH}_{\text{CaCL}_2}$ for utilisation of phosphate was indeed just above 5. Above this value, phosphate supply was restricted by decreasing rate of uptake by roots; below this value toxicity of aluminium toxicity became important. This paper reports an extension of these experiments to a plant that might be expected to differ: chickpea (*Cicer arietinum*).

Chickpea is an example of plants whose roots are known to secrete organic anions. The roots of many plants do this, and there is strong evidence that this improves their access to soil phosphate. Often secretion is mediated via cluster roots. These are ephemeral, closely-spaced groups of short roots. They secrete a burst of organic anions, especially citrate, and then die off (Shane and Lambers 2005). There are also plants that are known to secrete organic anions but without forming cluster roots. Chickpea (*Cicer arietinum*) is a frequently investigated example. Veneklaas et al. (2003) and Wouterlood et al. (2004a, b) found that it secreted mainly malonate, about 20% citrate, and a small amount of malate. Pang et al. (2018) studied a hundred genotypes and found that the mixture of carboxylates secreted averaged about 75% malonate, with acetate citrate and malate making up the balance. The results of Ohwaki and Hirata (1992) are slightly different; they found citrate was the largest fraction followed by malate and malonate. There is little information on the effects of such secretion on soil pH and on the uptake of phosphate.

It is widely reported that plants respond to P deficiency by acidifying the rhizosphere. For example, “Under low P, plant roots release organic acids to acidify the rhizosphere” (Lei et al. 2015). This is not always so. Most reports of decreased rhizosphere pH are for plants growing in soils or solutions of medium or high pH. One example is for lupin and maize growing in a calcareous loess subsoil (Ma et al. 2021). Another is for Faba beans growing in two calcareous soils (Baccari and Krouma 2023) In solution culture, Neumann and Römheld (1999) found that for tomato and chickpea, but not wheat, the pH of the solution dropped sharply from an initial value of 7 upon onset of P deficiency. Moorby et al. (1988) showed that when rape plants (*Brassica napus*) were deprived of P, the pH behind the root tip declined by up to 0.7 units below the initial value of 6.2.

There are some reports that are inconsistent with the generally accepted theory. Most remarkably, Wen et al. (2017) found that that rhizosphere acidification

was not induced by P deficiency but increased with increasing shoot P concentration. Similarly, Tang et al. (2009) found that for soybean plants growing in solution culture at pH 5.5, proton release increased with increasing phosphate supply. Nor is acidification universally observed. For roots of rape plants growing in a culture solution at pH 5.8 acidification was limited to a zone of about 1.5 cm just behind the root tip; for the rest of the solution the pH increased (Hoffland et al. 1989). It would be counter-productive to lower the pH further if it were already low. This is what Youssef and Chino (1989) found. They measured changes in the pH around roots of barley (*Hordeum vulgare*). When the initial pH was either above 8 or about 7, the rhizosphere pH decreased, but when the initial pH was about 5, the rhizosphere pH increased.

In this paper, we report an experiment in which we measured phosphate response curves for two cultivars of chickpea, at four different initial pH values, supplying them with nitrogen either as nitrate or as ammonium. We used different sources of nitrogen because we expected them to have different effects on the rhizosphere pH. We measured plant weight, plant P concentration, and rhizosphere pH. We thought that if chickpea roots acidified the rhizosphere, the optimum initial pH would be higher than that previously observed. Further, if organic anions complexed aluminium, chickpea might be better able to tolerate low pH.

Methods

We used two cultivars of chickpea. One is Anuradha. This variety was previously recommended by the West Bengal government and was widely used for a long time. It is now being replaced by improved lines, one of which is AGBL 184 (Sinha et al. 2018). Both cultivars belong to the Desi group, with compound leaves and small seeds. The weight per 100 seeds of Anuradha was 9.4 g and that for AGBL 184 was 11.1 g. The P content of seeds was 4.99 mg g⁻¹ for Anuradha and 6.04 mg g⁻¹ for AGBL 184.

The soil used

We used a soil from the Regional Research Station of Bidhan Chandra Krishi Viswavidyalaya at Jhargram in West Bengal, India (22°26'58.99"N,

86°59'49.23"E). This soil was previously used by Barrow et al. (2020). As indicated there, the soil was collected from well-drained site which was not used for cultivation. The average annual rainfall is 1400 mm, 81% of which falls in the monsoon months from June to early October. We collected bulk soil from the upper 20 cm during the dry season, in January 2019. We ground and mixed the soil well and passed it through a 2 mm sieve. The soil is classified as a coarse loamy Typic Haplustulf (USDA Soil Staff Survey 1999) or an Orthic Acrisol (FAO WRB 2006) in the red and lateritic soil zone. Some of its properties are: Colwell P, 11.4 mg kg⁻¹ (Colwell 1963); Bray P, 3.17 mg kg⁻¹ (Bray and Kurtz 1945); water holding capacity 28% (Piper 1966); organic C content, 3.1 g kg⁻¹ (Walkley and Black 1934). The pH_{CaCl2} was 3.91.

Modifying the pH of soil

To raise the pH of soil to three different levels, we added powdered CaCO₃ to subsamples of soil and moistened. We incubated the samples at 60 °C for 2 days to accelerate the reaction with lime (Barrow and Cox 1990). The amounts of CaCO₃ added were: 0, 5, 10 and 25 mmol kg⁻¹. This gave us four soils with pH_{CaCl2} levels of 3.9, 4.8, 5.8 and 7.1. We also modified the pH of the bulk soil. We mixed it with 7.5 mmol CaCO₃, moistened it, and allowed it to react for several weeks before drying it ready for use. The pH_{CaCl2} was 5.2.

Cultivating the plants

We grew plants in non-draining, deep, black plastic bags of 1 kg capacity. We divided each of the four soil samples of different pHs into two sets for two cultivars of chickpea used. Because the supplies of bulk soil were limited, we first added 200 g of acid-washed white river sand. Over this, we added 500 g of bulk soil of pH_{CaCl2} 5.2 and then 300 g of soil for which the pH had been modified and for which appropriate samples had been treated with P using KH₂PO₄ solutions. For each pH there were ten levels of P. There were two sources of N: ammonium and nitrate. Thus, for each pH and each genotype there were 20 bags. We wetted the soil to field capacity and sowed ten seeds of chickpea. After germination we kept five healthy plants in all the bags. This means that the

amount of P added in the seeds was (mg per pot⁻¹) Anuradha, 2.5, AGBL 184, 3.3. Seven days after germination, we added 20 mL nutrient solution containing the following basal nutrients (mg nutrient pot⁻¹): Mn 3.2, Mo 0.8, Cu 0.8, B 0.16, Zn 8, Mg 4.8, K 80 and N 80. The amount of K added was adjusted after calculating the amount added through KH₂PO₄. We irrigated the plants with deionised water as required. The experiment was carried out in a net house on a roof top.

We cut the above ground parts at ground level 34 days after germination, washed them in 0.01 M HCl and then in deionised water. We weighed the plants after drying in a hot air oven at 60 °C to constant weight. Subsamples of 100 mg were digested using a concentrated HNO₃–HClO₄ (v/v=3:1) mixture for estimation of P concentrations (Murphy and Riley 1962).

We cut open the bags containing soil and roots and gently shook the plants to remove bulk soil. We regarded the soil adhering to the roots as rhizosphere soil. We cut off ten apical parts of lateral roots of 40 mm in length along with adhered soil. These were placed in pre-weighed beakers and the weights of samples were recorded. We added appropriate volumes of 0.01 M CaCl₂ solution to give a weight: volume ratio of 1:2.5 and measured the pH of this solution after allowing some time.

Describing the results

For each treatment combination, the responses were described by an equation of the form:

$$Y = a(1 - \exp(-c(x + d))) \quad (1)$$

where Y is a measure of the productivity such as dry matter produced, x the P supplied, and the other symbols are parameters. This is a form of the Mitscherlich equation. The parameter a indicates the maximum to which the plant weights trend. The parameter d is formally the extrapolation of the response curve and may be interpreted as an estimate of the P supplied by the soil. The parameter c reflects the plants effectiveness in responding to P; the larger its value, the smaller the amount of P required for a given plant weight. If f indicates a fraction of the maximum plant weight, we can calculate the fertiliser required to meet that fraction. From Eq. 1, this is

$$x + d = \ln(1 - f)/c. \quad (2)$$

The value of c is therefore an indicator of the P required for a given fraction of the plant weight.

This equation was fitted using SigmaPlot 10.

When plant weights were related to the rhizosphere pH, the parameters a and c were replaced by functions of rhizosphere pH (Fig. 5). These equations were fitted using a program written in GW BASIC.

Results

Responses to phosphate (Fig. 1) were strongly affected by the soil's initial pH. At the lowest value ($\text{pH}_{\text{CaCl}_2}$, 3.9), response was markedly lower; maximum plant weights were not approached until at least $150 \text{ mg P pot}^{-1}$ had been applied. Response was also weak when the initial $\text{pH}_{\text{CaCl}_2}$ was 4.8. Strongest response occurred when the initial $\text{pH}_{\text{CaCl}_2}$ was 5.9;

maximum plant weights were approached at about 40 mg P pot^{-1} .

Figure 2 shows that in most cases there was little effect of nitrogen source on response to P. The two exceptions were for the Anuradha cultivar; at low pH, nitrate produced bigger yields, at high pH, ammonium produced bigger plant weights.

AGBL 184 cultivar approached maximum plant weights that were a bit more than 20% greater than those for Anuradha cultivar. This is approximately the ratio of their seed weights, and this suggests relative growth rates were similar.

Figure 3 suggests that the AGBL 184 cultivar used the applied phosphorus slightly more effectively because the values for the c coefficient were slightly higher; the larger the value of c , the smaller the amount of P required for a given plant weight (Eq. 2). However, the c and d parameters are correlated; high values for one can be largely offset by low values for the other. This cultivar had low

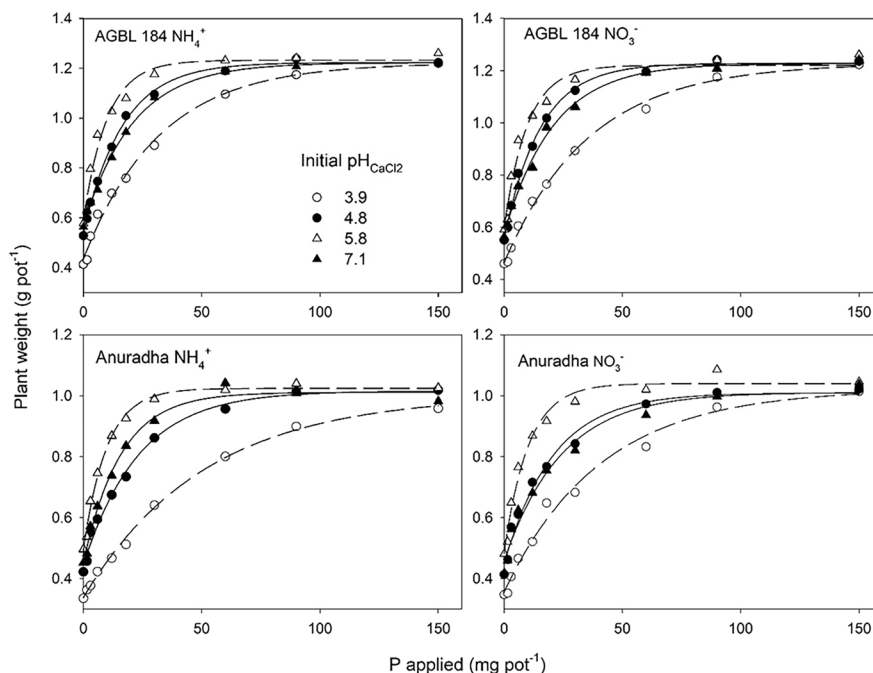


Fig. 1 Effects of initial pH and of nitrogen source of the response of two cultivars of chickpea to phosphorus in a pot trial. For each treatment combination, the responses are described by an equation of the form: $Y = a(1 - \exp(-c(x + d)))$ where Y is the plant weight, x the P supplied, and the other symbols are parameters. The parameter a indicates the maximum to which the plant weights trend, as can be

seen from the graph. The parameter c reflects the plants effectiveness in responding to P; the larger its value the smaller the amount of P required for a given plant weight. The parameter d is formally the extrapolation of the response curve and may be interpreted as an estimate of the P supplied by the soil and seed. The values for c and d are shown in Fig. 3

Fig. 2 Comparison of the effects of nitrogen source and of cultivar on the response to P by chickpea. The curves showing the fitted plots are from Fig. 1

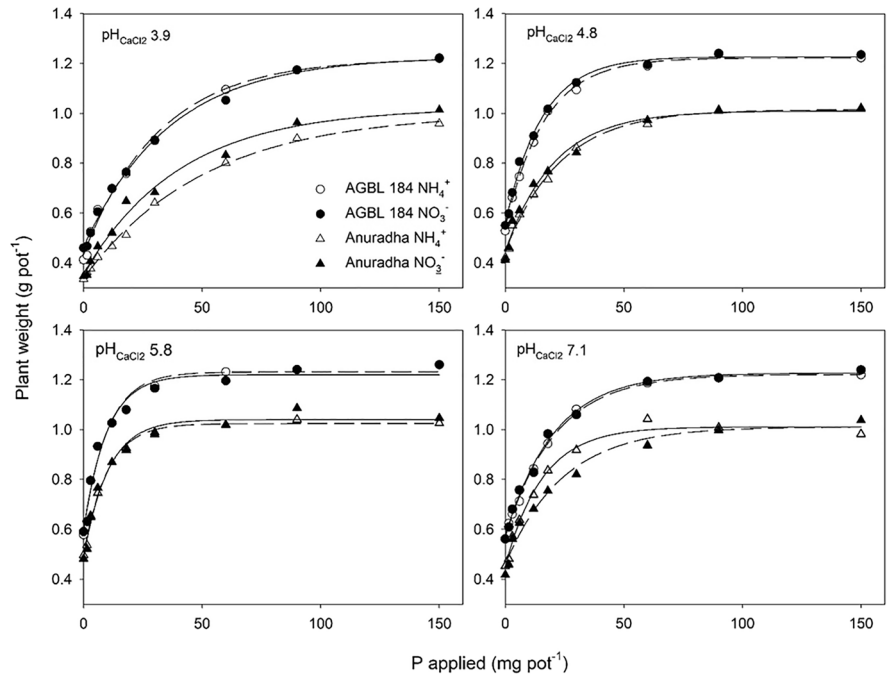
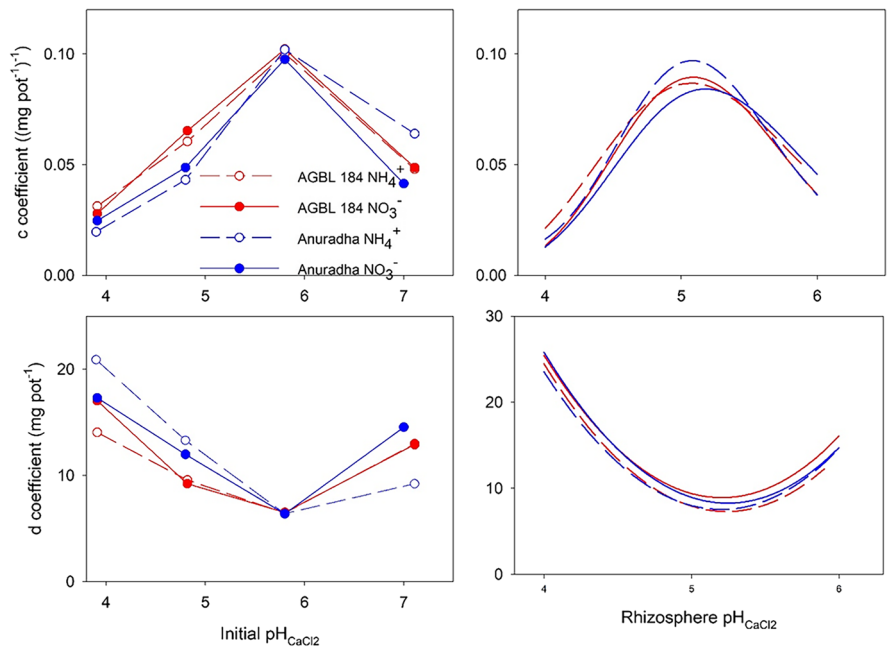


Fig. 3 Values of the parameters *c* and *d*. In the left-hand panels values derived from Fig. 2 and are plotted against the initial pH. In the right-hand panels they are derived from Fig. 6 and are plotted against the rhizosphere pH

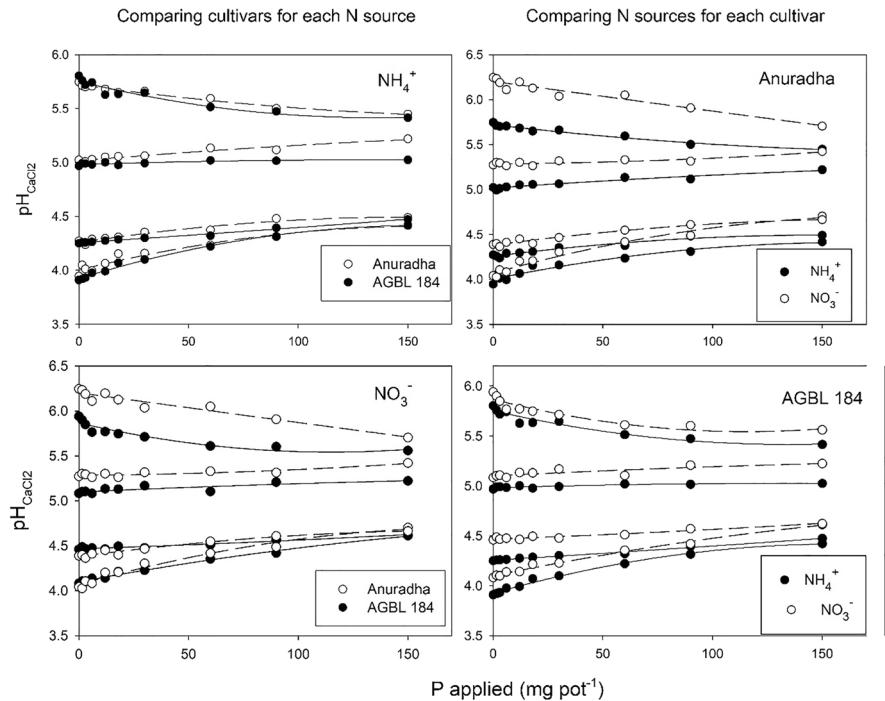


values for the *d* parameter, so the net effect was small. This figure also shows that the *d* parameter, which represents the P derived from soil and seed, formed a V-shaped relationship with pH. A similar effect has been reported for mustard, lucerne, and rice by Barrow et al. (2020).

There were large effects of P supply on the rhizosphere pH (Fig. 4). At low initial pH the rhizosphere pH increased with P supply; at high initial pH it decreased.

For the AGBL 184 cultivar the rhizosphere pH was generally lower than that for the Anuradha cultivar

Fig. 4 Effect of amount of P applied on the rhizosphere pH as affected by nitrogen source and cultivar

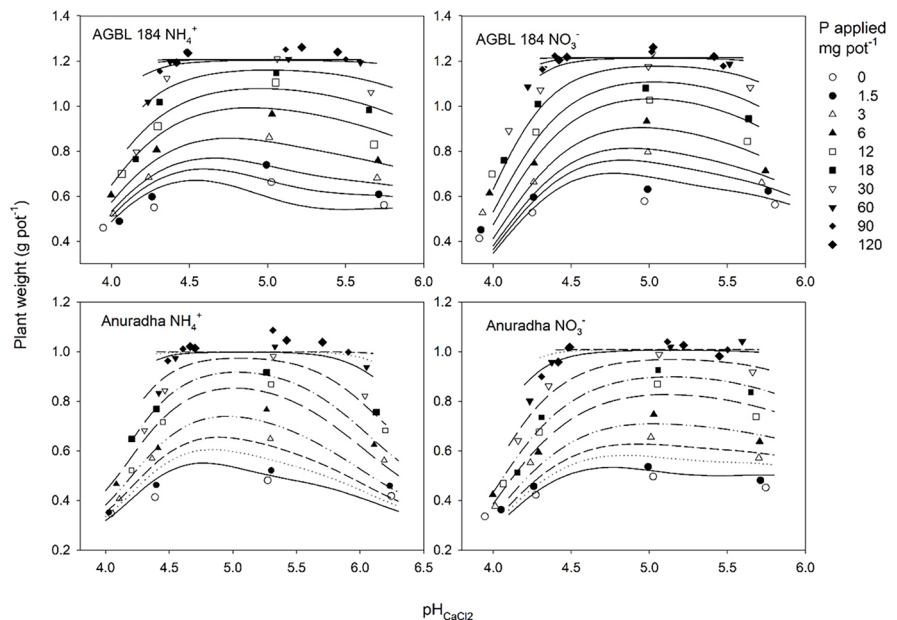


(Fig. 4). The effects were largest where nitrogen was supplied as nitrate at high initial pH. This differs from the results of Veneklaas et al. (2003) who found that three commonly used Western Australian chickpea cultivars had very similar rhizosphere carboxylate concentrations.

The rhizosphere pH was generally lower when nitrogen was supplied as ammonium (Fig. 4). The effects were largest for the Anuradha cultivar at high pH.

In Fig. 5, dry matter produced is plotted against the rhizosphere $\text{pH}_{\text{CaCl}_2}$. Production was lowest at lower

Fig. 5 Relationship between the rhizosphere pH and plant growth at 10 levels of applied P. The lines fitted are for a global equation for each panel. For these equations, the c and d parameters are replaced by functions of pH. For the c parameter a lognormal equation was used: $c = a_1 + b_1 - 0.5(\ln(\text{pH} / c_1) / d_1)^2$ for the d parameter, a quadratic equation was used: $d = a_2 + b_2 \text{pH} + c_2 \text{pH}^2$ and $Y = a(1 - \exp(-c(x+d)))$ as for Fig. 2



pH and highest near $\text{pH}_{\text{CaCl}_2}$ 5. These responses are summarised in Fig. 3. This figure shows that effectiveness was lowest at low pH and highest at just above $\text{pH}_{\text{CaCl}_2}$ 5.

Plots of plant weight against P concentration in the tissue are used to test whether growth is solely limited by P supply. When this is the case, plots fall close to a common line. Figure 6 shows that this was so for three of the initial pH values. For the initial $\text{pH}_{\text{CaCl}_2}$ of 3.91, plots fell slightly below the others. We think this indicates only a small effect of aluminium toxicity.

Discussion

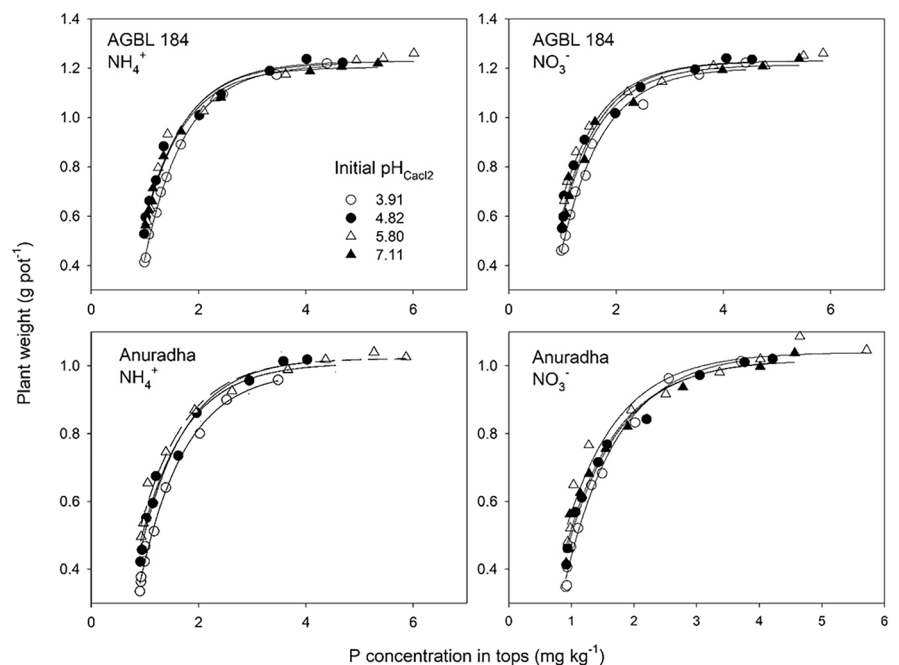
Effects on pH

The effects of our treatments on the rhizosphere pH of chickpea were unusual in two respects. One is that at high initial pH, the rhizosphere pH decreased, but at low initial pH the rhizosphere pH increased. There is much emphasis on the effects of plants in decreasing the rhizosphere pH, as occurred here at high initial pH, but few observations of an increase in pH at low initial pH. To decrease the pH when it is already low would be counter-productive.

The other unusual aspect is that these effects on rhizosphere pH were closely related to the phosphate supply. The greater the supply, the greater the decrease at high pH and the greater the increase at low pH. Wen et al. (2017) observed a similar effect of P supply at high pH, and Tang et al. (2009) showed that when pH was maintained at 5.5, proton release increased with increasing P supply. However, our results show that at low pH the direction of the effect was different; with increasing P supply, pH increased. We think that this observation is inconsistent with one of the theories put forth by Wen et al. (2017). They explain the decrease in pH as being the result of increased shoot K^+ accumulation with increased release of protons. Tang et al. (2009) showed that proton by chickpea was closely correlated with anion-cation balance. There are several reports of similar effects for other species, for example Tang et al. (2004). We question whether these effects can be the only cause in our case. We suggest an additional mechanism.

Consider the way all plants take up phosphate. Not only is this against a very steep concentration gradient, but it is also through a negatively charged membrane. There is strong evidence that uptake is accomplished by co-transporting phosphate ions and hydrogen ions (Sakano 1990; Rausch and Bucher

Fig. 6 Effects of initial pH and of nitrogen source on the relationship between plant growth and tissue P concentration for two cultivars of chickpea



2002). Some of the hydrogen ions are then expelled by a proton pump. The expulsion does not necessarily balance the inflow. Sakano (1990) found that phosphate uptake caused the pH of the medium to increase from pH 3.5 to values as high as 5.8, with corresponding decreases in the pH of the cytoplasm. Further, the proton balance depended on the loading; as the loading increased the ratio of protons expelled decreased; that is there was a feedback mechanism. Ulrich and Novacky (1990) also observed pH decreases in the cytoplasm on uptake of phosphate. These effects would explain our observed increase in rhizosphere pH when the initial pH is low. To explain the decrease in rhizosphere pH when the initial pH is high, we suggest that chickpea has evolved a mechanism by which the activity of the proton pump depends on the external pH.

It follows that the uptake mechanism for phosphate in chickpea is such that there is a net import of protons at low pH and a net export at high pH. The rhizosphere pH trended towards a value of about 5 from both low and high initial values.

We add the obvious caveat; there are, as yet, but few results. We do not know under what circumstances these results occur nor how many different plants behave in this fashion. Surely a field for further research.

We find it intriguing that a similar effect occurs when phosphate reacts with soil: at initial $\text{pH}_{\text{CaCl}_2}$ above five, reaction with P decreases the pH; at initial $\text{pH}_{\text{CaCl}_2}$ below five, reaction with P increases the pH (Barrow et al. 2021). There are analogies between the two effects; both can be interpreted in terms of the way that charge on the reacting phosphate ions is balanced, but the mechanism involved in this balance differs.

Effects of pH

The marked decrease in pH when the initial pH was high, means that best growth occurred when the initial $\text{pH}_{\text{CaCl}_2}$ was 5.8, and this was associated with a lower rhizosphere pH. Best growth occurred when the rhizosphere $\text{pH}_{\text{CaCl}_2}$ was about 5. For lucerne, rice and mustard, this was close to the optimum initial value (Barrow et al. 2020).

For chickpea, plots of the c coefficient against $\text{pH}_{\text{CaCl}_2}$ are almost mirror images of those for lucerne, mustard and rice (Fig. 7). For chickpea, there is a long upward slope followed by a short downward slope; for lucerne, mustard and rice, the opposite is the case. Thus, in contrast to our expectations, chickpea growth was more decreased by low pH than that of the other species. This was not a consequence of

Fig. 7 Comparing the effects of pH on the c coefficient for chickpea with those for lucerne mustard and rice. The c coefficient is a measure of the effectiveness of the fertiliser; the larger its value, the smaller the amount of P required for a given plant weight. The upper plots are based on plant weight, lower ones on P uptake

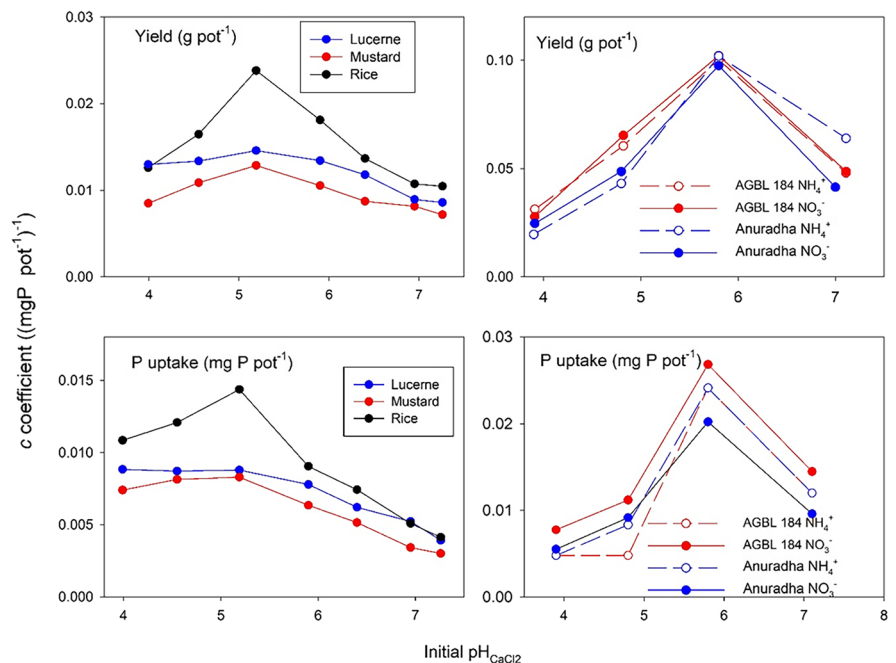
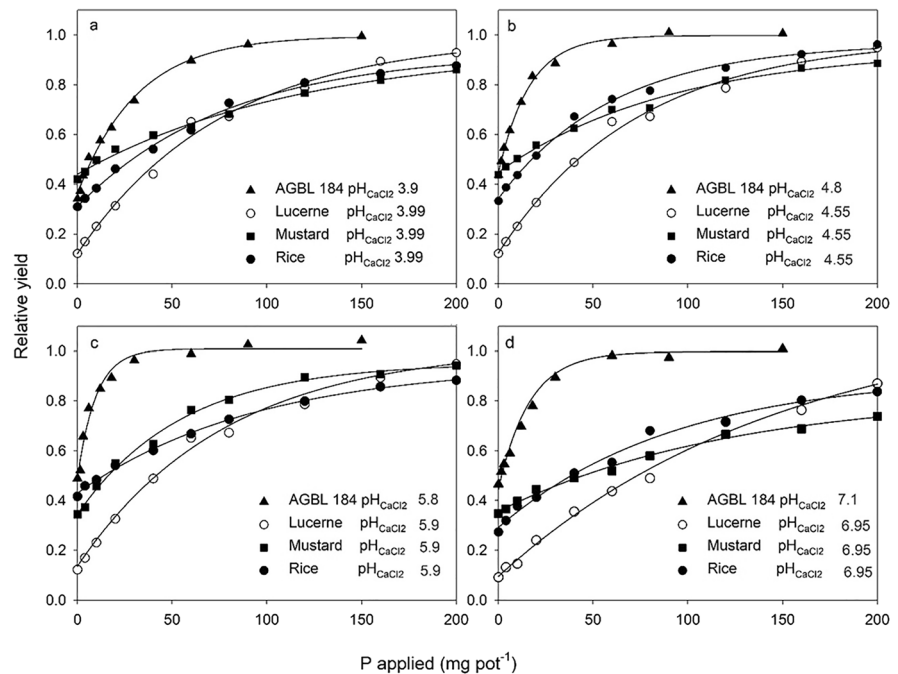


Fig. 8 Comparing the response curves to phosphate for lucerne, mustard (Barrow et al. 2020) and rice with those for a chickpea cultivar. In each case the comparison is for the nearest available pH. The relative yield is the yield expressed as a fraction of the maximum as obtained in the equation fitted for each species



greater effect of aluminium; indeed, there seemed to be less effect of aluminium toxicity (Fig. 6). We are aware of the problems of making comparisons across experiments, but we think the effects are so large that these are real differences. Our results are consistent with our suggestion that the uptake mechanism for chickpea differs from that of the other species.

Organic anions

Here, we discuss the possible relationships between our results and the known secretion of organic anions by chickpea roots.

In our studies of the displacement of phosphate by citric acid (Barrow et al. 2017), we found that the main mechanism was competition between citrate ions and phosphate ions for sorption. Citrate is an effective competitor because, like phosphate, it can form bidentate links with an oxide surface. Its effectiveness is proportional to the concentration of its divalent ions in the solution. This depends partly on the dissociation characteristics of the acid and partly on the concentration of cations in the solution. Calcium ions are particularly important because they are common in soil and because calcium forms complexes with carboxylic anions especially at high pH (Barrow et al. 2017). The presence of calcium

decreases the pH at which maximum concentration of divalent ions occurs (Barrow et al. 2017). The $\text{pH}_{\text{CaCl}_2}$ at which citric ion was most effective at displacing phosphate was about 4. Although it is often thought that citrate is effective because it is a tricarboxylic acid, the third acid group plays no direct role in the reaction (Barrow et al. 2017). Its main effect is to increase the propensity for the other acid groups to dissociate; the $\text{pK}_{\text{a}2}$ for citric acid is 4.76, that for malonic acid is 5.69. Extrapolation would suggest that malonic acid might be most effective at $\text{pH}_{\text{CaCl}_2}$ of about 5. Perhaps it is not entirely a coincidence that this is the pH at which chickpea roots were most effective in obtaining phosphate.

How P effective is chickpea?

Figure 8 presents a direct comparison between the response of chickpea to P and that for lucerne, rice and mustard at similar pH values. We are aware that this comparison involves different experiments and therefore should be treated with caution. However, we think this comparison shows an important effect. Because the effects of pH differ, the advantage to chickpea is greatest when the initial $\text{pH}_{\text{CaCl}_2}$ was close to 7. This reflects the considerable depression in response at high pH for lucerne, rice and mustard.

Declarations

Author contributions AD designed the experiment, supervised the work, helped analyse the data and wrote parts of the manuscript. SAP carried out the experiment. NJB completed the data analysis and wrote most of the paper.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests We have no relevant financial or non-financial interests to disclose.

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